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Age, year-class strength variability, and partial age validation of *Coregonus kiyi* from Lake Superior

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Abstract

Age estimates of Lake Superior Kiyi *Coregonus kiyi* from scales and otoliths were compared and 12 years (2003-2014) of length frequency data were examined to assess year-class strength and validate age estimates of Kiyi. Ages estimated from otoliths were precise and were consistently older than ages estimated from scales. Maximum otolith-derived ages were 20 for females and 12 for males. Age estimates showed high numbers of fish aged 5, 6, and 11 in 2014, which correspond to the 2009, 2008, and 2003 year-classes, respectively. Strong 2003 and 2009 year-classes, along with the 2005 year-class, were also evident by distinct modes of age-1 fish (<110 mm) in the length frequency distributions from 2004, 2010, and 2006, respectively. Modes from these year-classes were present as progressively larger fish in subsequent years. Few to no age-1 fish (<110 mm) were present in all other years. Ages estimated from otoliths were generally within one year of ages corresponding to strong year-classes, at least for fish age-5 and older, suggesting that Kiyi age may be reliably estimated to within one year by careful examination of thin-sectioned otoliths.

<A>Introduction

Kiyi *Coregonus kiyi* is one of eight cisco species (*C. alpenae*, *C. artedi*, *C. hoyi*, *C. johannae*, *C. nigripinnis*, *C. reighardi*, and *C. zenithicus*) that historically existed in the Laurentian Great Lakes (Koelz 1929). Kiyi were found in Lakes Huron, Michigan, Ontario, and Superior (Koelz 1929), but presently occur only in Lake Superior (Eshenroder et al. 2016). The demise of Kiyi in the other Great Lakes is not well understood, but may have been due to increased abundances of Alewife *Alosa pseudoharengus* and Rainbow Smelt *Osmerus mordax* (Christie 1974), overfishing (Moffet 1957; Smith 1964; Parker 1989), or introgression to a generic deepwater cisco swarm by interbreeding with other deepwater cisco species (Eshenroder et al. 2016). In contrast to Lakes Michigan and Huron, Kiyi in Lake Superior appear to have retained their morphological characters and have not introgressed to a species swarm (Eshenroder et al. 2016). Kiyi is presently the most abundant deepwater (>100 m) pelagic species in Lake Superior (Yule et al. 2013).

Accurate age estimates are fundamental to understanding the life history and population dynamics of fish (Beamish and McFarlane 1983). However, age estimation can be difficult for long-lived fishes because of crowded annuli on the margins of calcified structures due to slow growth (Campana 2001). Systematic underestimation of fish age can lead to overestimates of growth and mortality rates (Mills and Beamish 1980) and compromise understanding of year-class strength (Yule et al. 2008). Maximum reported ages of Kiyi in earlier studies using scales were 6 years from Lake Ontario (Pritchard 1931) and 10 years from Lake Michigan (Deason and Hile 1947). More recent otolith-based maximum age estimates for Lake Superior Kiyi were >20 years (Gorman 2012; Pratt and Chong 2012). These results agree with others who found that age estimates derived from otoliths and fin spines or rays typically exceed age estimates derived from scales (Maceina et al. 2007; Quist et al. 2012). A comparison of scale and otolith-derived ages of Kiyi has not been conducted, nor have the ages of deepwater ciscoes been validated, *sensu* Beamish and McFarlane (1983).

High interannual variation in year-class strength was not historically described for Laurentian Great Lakes cisco species (Koelz 1929). Dryer and Beil (1964) observed a minor 2 to 3-fold fluctuation in year-class strength in Lake Superior Cisco *C. artedi* based on commercial fishery landings from 1950-59 and scale-derived age estimates. Later work evaluating Cisco populations in Lake Superior (Hoff 2004; Stockwell et al. 2009; Rook et al. 2012; Myers et al. 2015) and

Bloater *C. hoyi* populations within Lakes Huron, Michigan, and Superior (Bunnell et al. 2010) showed large 10 to 2,795-fold differences in year-class strength as measured by densities of age-0 or age-1 fish. Yule et al. (2008) showed how age underestimation associated with scale-derived ages could lead to an inaccurate understanding of the regular production of strong year-classes of Lake Superior Cisco. Interannual variability in Kiyi year-class strength has not been evaluated.

The purpose of this study was to 1) compare Lake Superior Kiyi ages estimated from scales and otoliths, 2) evaluate variability in year-class strength, and 3) assess the validity of otolith-derived Kiyi ages by comparing the distribution of age estimates to strong year-classes identified from annual length frequency distributions.

<A>Methods

Age analyses. –

Fish collections were made at 102 locations throughout Lake Superior (Figure 1) during daylight between 19 May and 20 July 2014. Collections were made with the U. S. Geological Survey Research Vessel Kiyi using a Yankee bottom trawl with either a chain or rubber disk foot rope towed at approximately 3.5 km/h. Both nets had an 11.9 m head rope, 15.5 m foot rope, and 2.2 m wing height with stretch meshes of 89 mm at the mouth, 64 mm for the trammel, and 13 mm at the cod-end. Nearshore trawling in May and June was cross-contour with a mean beginning depth of 19 m (range: 11-40), ending depth of 61 m (range: 19-144), and distance covered of 1.7 km (range: 0.5-3.8). Offshore trawling in July followed a constant depth contour with a mean average depth of 191 m (range: 92-315) and distance covered of 1.4 km (range: 1.2-1.5). Trawl distance was determined from the ship's geographic positioning system. Kiyi were identified based on morphological characteristics, such as fin length and eye diameter, as described in Koelz (1927) and Eshenroder et al. (2016). Individuals for which identification was ambiguous were not included in this study. All Kiyi collected were counted, weighed in aggregate, and frozen for later processing. Relative density (fish/ha) and biomass (kg/ha) were estimated by dividing collection counts and aggregate weights by the area swept by each trawl tow.

Frozen fish were thawed at room temperature before total length to the nearest mm, weight to the nearest gram, and sex (visually determined as female, male, or juvenile) were recorded. A lakewide representative sample for estimating age was obtained by selecting 10 individuals per

10 mm length bin from fish ≥ 160 mm collected in each of five regions (Figure 1). All fish <160 mm were selected for estimating age because fish of this size were rare. Otoliths were removed using the “up through the gills method” described by Secor et al. (1992). Scales were removed from either side of the fish directly above the lateral line as close to the anterior margin of the dorsal fin as possible (Hogman 1968). Scales and sagittal otoliths were placed in paper envelopes to air dry.

Otolith preparation followed the commonly used (Quist et al. 2012) “embed and polish” method described by Secor et al. (1992). Otoliths were embedded in clear epoxy (Buehler EpoKwick™ Epoxy, 5:1 ratio of resin to hardener) before a 0.5-mm thick section through the nucleus along the dorsoventral plane was obtained with a Buehler IsoMet™ Low Speed Saw. Otolith thin sections were lightly polished with 1000-grit sandpaper before viewing in mineral oil on a black background with reflected light applied at approximately a 45 degree angle to the section. A digital image of each thin section (Figure 2) was captured with a Nikon DS-Fi2™ camera attached to a Nikon SMZ745T™ stereo microscope. Multiple images were used for some otolith sections where a single image that was clear and focused in all areas could not be obtained. Age estimates were also obtained from scales for fish collected from the eastern Michigan region. Age was estimated from scales for a limited number of fish because a clear difference in age estimates between scales and otoliths was expected, as shown for numerous other fish including other coregonines (e.g., Maceina et al. 2007; Yule et al. 2008; Quist et al. 2012; Stewart et al. 2016). Digital images were captured from scales pressed into 5-mm thick acetate slides with the same camera and microscope described for otoliths.

Two readers, who were blind to any biological information related to the fish, identified annuli on scales and otoliths from the digital images. One reader had approximately 25 and the other reader had approximately two years of previous experience estimating age from scales and otolith thin sections. The inexperienced reader was, however, trained to estimate age on Kiyi scales and otolith thin sections that were not included in this analysis. The combination of a translucent band representing fast growth and an opaque band representing slow growth on the sectioned otolith was interpreted as one year of growth (Figure 2). Only a completed opaque band at the otolith margin was counted as an annulus, as partial growth from the capture year was present for some individuals. Annuli on scales were identified using “cutting-over” and “compaction” characteristics evident in the circuli (Quist et al. 2012). After initial analyses that

compared age estimates between readers (see below), the two readers further reviewed the scale or otolith image to achieve a consensus age estimate for analyses that required a single estimate of age.

Bias in scale-derived and otolith-derived age estimates between two readers (e.g., one reader consistently estimated lower ages than the other reader) and between consensus scale and otolith-derived age estimates was assessed with the Evans and Hoenig (1995) test of symmetry for the age-agreement table (as suggested for use by McBride 2015), modified age-bias plot (Campana et al. 1995; Muir et al. 2008a), and 1-sample t-test that tests if the mean difference in ages at each reference age differed from zero (Ogle 2016). Reference ages for age-bias plots and 1-sample t-tests were ages estimated by the more experienced reader or from otoliths. The method of Holm (1979) was used to adjust for multiple comparisons in the 1-sample t-tests. The 1-sample t-tests were not computed when the sample size was less than three. Precision between readers was summarized as the percentage of fish for which the ages differed by zero or by one or fewer years and the average coefficient of variation (Chang 1982; Kimura and Lyons 1991). Age bias and precision metrics were computed with the `ageBias` and `agePrecision` functions, respectively, from the FSA package v0.8.13 (Ogle 2017) in the RTM statistical environment v3.4.0 (R Development Core Team 2017). All tests used $\alpha=0.05$ to determine statistical significance.

An age-length key (Fridriksson 1934; Ketchen 1949) was constructed from consensus otolith-derived age estimates. The age-length key was then used to assign specific ages to all Kiyi captured in 2014 using the method described by Isermann and Knight (2005) as implemented in the `alkIndivAge` function from the FSA package.

Length frequency year-class identification. –

Annual Kiyi length frequency data from the same locations and months and collected using the same methods were available from nearshore sites from 2003-2014 and from offshore sites from 2011-2014 (Vinson et al. 2016). Length frequency distributions from these years were visually examined for evidence of strong year-classes (i.e., recruitment) which could be used to assess the validity of the estimated ages for Kiyi captured in 2014. Kiyi likely hatch at a size (10-12 mm) and time (spring) similar to Cisco (Oyadomari and Auer 2007, 2008) and were likely not present as age-0 fish in these annual trawl samples. In Lake Michigan, Kiyi reached a mean standard length of approximately 100 mm the following spring at age-1 (Deason and Hile 1947).

Thus, clusters of fish in our annual spring and summer collections with distinct modes less than 110 mm total length were identified as age-1 fish. The relative numbers of age-1 fish in these samples was used as an index for the strength of the previous year's year-class of Kiyi.

Results

A total of 984 Kiyi were collected at 24 of the 102 locations sampled in 2014 (Figure 1). Kiyi were found at three nearshore locations between 27 May 2014 and 5 June 2014, and at 21 offshore locations between 7 July and 20 July 2014. Biomass and density estimates from individual trawl tows ranged from 0-12 kg/ha and 0-253 fish/ha, respectively. The minimum and maximum depths of capture at 21 on-contour sampling locations were 132 and 256 m. Maximum biomass (12 kg/ha) and density (253 fish/ha) were observed at 190 m. Kiyi total lengths ranged from 108-266 mm with a mean of 197 (SD, 19.3) mm.

Age analyses

Ages in 2014 were estimated from 62 pressed scales. A consensus age was reached for all scales. Scale-derived age estimates from the two readers agreed for 46.8% of the fish, agreed within one year for 87.1% of the fish, and had an average coefficient of variation of 8.7. A statistically significant bias was evident in scale-derived age estimates between readers ($P=0.009$; Figure 3). The inexperienced reader generally estimated age from scales to be one year younger when the experienced reader's estimate was 6 or older, though this was only statistically significant at age-6 (95% CI: 4.65-5.49; $P=0.002$).

Ages in 2014 were also estimated from 288 thin-sectioned otoliths. Of these, 22 (7.6%) otoliths were deemed unreadable (cracked or cloudy image) and were removed from further consideration. There was no statistically significant systematic bias in otolith-derived age estimates between the two readers ($P = 0.445$; Figure 4), though the mean estimated age for the inexperienced reader was slightly greater when the experienced reader estimated an age of 5 (95% CI: 5.1-5.4; $P < 0.001$) and slightly lower when the experienced reader estimated an age of 12 (95% CI: 11.1-11.8; $P = 0.031$). Otolith-derived age estimates from the two readers agreed perfectly for 72.6% of the fish, agreed within one year for 97.0% of the fish, and had an average coefficient of variation of 2.8.

A statistically significant bias was detected between consensus scale- and otolith-derived age estimates ($P < 0.001$; Figure 5). Mean consensus scale-derived age estimates were less than the consensus otolith-derived age estimate for the same fish for all five ages with a sample size of at least three ($P < 0.008$).

The maximum estimated age was 20 for females and 12 for males from otoliths and 8 for both females and males from scales. The minimum estimated age was 4 from otoliths and 3 from scales for both females and males. The distribution of otolith-derived age estimates for Kiyi captured in 2014 showed distinct modes at age 11 and ages 5 or 6 (Figure 6), which correspond to the 2003, 2008, and 2009 year-classes.

Length frequency year-class identification

Examination of length frequency distributions from Kiyi captured in 2003-2014 showed that clusters of fish with a mode < 110 mm were present in high numbers in 2004, 2006, and 2010 and were not detected or were at very low numbers in all other years (Figure 7). The fish in these clusters correspond to the 2003, 2005 and 2009 year-classes, respectively. The cluster of Kiyi in the 2003 year-class was distinct in subsequent years until at least 2006. In 2007, the cluster of Kiyi from the 2005 year-class were either not evident or had grown enough to be indistinguishable from Kiyi of the 2003 year-class. Kiyi from the 2009 year-class were still distinct in 2010 but were either not evident or had grown enough to be indistinguishable from older fish by 2013. Only one distinct mode was evident in the length frequency distribution from 2014.

<A>Discussion

Precision between readers for thin-sectioned otoliths was very good as the average coefficient of variation (2.8) was less than 5, which Campana (2001) suggested represented “high precision.” This result was somewhat surprising because both readers expressed difficulty interpreting putative annuli near the center of otoliths when few annuli were present (i.e., relatively young fish) and at the margin on all otoliths (Figure 2). Due to the sporadic production of year-classes, no fish with an otolith-derived age less than four were collected in 2014. Without these young fish, an understanding of the appearance of the first few annuli could not be developed. Interpretation of the otolith margin is notoriously difficult (Campana 2001) and a

better understanding of the otolith margin also could not be developed because our samples were restricted to two days in early June and a few days in mid-July, rather than throughout the May to September growing season. However, length frequency distributions for three other years when Kiyi were sampled in several months suggested that substantial growth in length of Lake Superior Kiyi was not evident until at least late July. This suggests that little current season's growth should have been observed on the otolith thin sections in our sample. However, 21% and 36% of the otoliths were categorized by reader 1 and reader 2, respectively, as having evidence for growth in the current season.

Kiyi ages estimated from otoliths were consistently greater than ages estimated from scales. This is consistent with previous results for Lake Superior Cisco (Yule et al. 2008) and Pygmy Whitefish *Prosopium coulteri* (Stewart et al. 2016), Canadian Lake Whitefish *Coregonus clupeaformis* (Mills and Beamish 1980; Barnes and Power 1984) and Round Whitefish *Prosopium cylindraceum* (Jessop 1972), Lake Michigan Lake Whitefish (Muir et al. 2008b), Lake Huron Lake Whitefish (Muir et al. 2008a), European Vendace *Coregonus albula* (Aass 1972), as well as for many other fish (Maceina et al. 2007; Quist et al. 2012). Our maximum otolith-derived age estimates of 20 for females and 12 for males is similar to Pratt and Chong (2012) who observed maximum otolith-derived age estimates of 22 for females and 16 for males from Kiyi collected in Canadian waters of Lake Superior and Gorman (2012) who reported Lake Superior Kiyi life spans as >20 years. These ages are similar to the maximum otolith-derived age estimates for Lake Superior Cisco (21 for female and 17 for male; Yule et al. 2008).

Distinct modes in length frequency distributions from 2003-2014 provided evidence for strong year classes and partially validate our otolith-derived age estimates. The mode of age-11 fish in 2014 corresponds well with the 2003 year-class and the mode of age-5 and 6 fish in 2014 corresponds, with some ageing error (see below), to the 2009 year-class present in the length frequency distributions. However, a mode of age-9 fish that would correspond to the 2005 year-class present in the length frequency distributions was not observed in 2014. This lack of age-9 fish in our 2014 age analysis could be attributed to the apparent smaller size of that year-class as compared to the 2003 and 2009 year-classes. Thus, with the exception of age-9 fish, our otolith-derived age estimates from 2014 were generally within one year of ages corresponding to strong year-classes of Kiyi.

Our determination of strong year-classes from the trawl-based length frequencies is dependent on the mode of the smallest fish being near 100 mm in total length. This primarily occurred only in 2004 and 2010. Kiyi likely hatch at a size (10-12 mm) and time (spring) similar to Cisco (Oyadomari and Auer 2007, 2008). In Lake Michigan, Kiyi reached a mean standard length of approximately 100 mm the following spring at age-1 (Deason and Hile 1947). Additionally, modal progression analysis (Du 2002) showed that the mean of the cluster of smallest fish in 2004 was 86 (SD=11) mm and had grown to 112 (SD=11) mm in 2005 and 137 (SD=11) mm in 2006. Similarly the mean of the cluster of smallest fish in 2010 was 83 (SD=7) mm and had grown to 120 (SD=10) mm in 2011. Given that the annual change in means of these clusters of fish is more than two times the SD, it is unlikely that growth would be poor enough that multiple year-classes would form one cluster at small sizes and then grow substantially together in subsequent years. Thus, these clusters of small fish in 2004 and 2010 are most likely only age-1 fish.

From these findings, it appears Kiyi age may be reliably estimated to within one year by examination of thin-sectioned otoliths. Ageing error may be reduced with a better understanding of the characteristics of the first few annuli and the appearance of the otolith margin. It is recommended that otoliths be collected from small (young) Kiyi in years when they are present and from Kiyi collected throughout the open-water growing season when feasible. Continued annual collections of length frequency data, along with otoliths from these fish, will allow for further validation of Kiyi age estimates from otoliths. Because otoliths appear to provide an accurate estimate of age, and age estimates from scales were less than that from otoliths for all otolith-derived ages, scales should no longer be used to estimate the age of Kiyi.

The annual length frequency distributions suggest that Kiyi experience high interannual variability in year-class strength. Only three strong year-classes were observed at age-1 from 2003-2014. Variable recruitment has been observed in other *Coregonus* spp. (e.g., *C. albula*, Axenrot & Degerman 2015; *C. artedi*, Hoff 2004; Stockwell et al. 2009; Myers et al. 2015; *C. autumnalis*, Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990; *C. hoyi*, Bunnell et al. 2006, 2010; Gorman 2012; Collingsworth et al. 2014; and *C. zenithicus*, Gorman 2012). Strong Kiyi year-classes in 2003, 2005, and 2009 correspond to higher than average year-class strengths of Lake Superior Bloater and Cisco (Stockwell et al. 2009; Yule et al. 2008; more recent data in Vinson et al. 2016). Recruitment synchrony has also been observed within Bloater (Bunnell et

al., 2006, 2010) and Cisco (Myers et al. 2015) populations across the Great Lakes and in Europe (Sandström et al. 2014). Hypothesized factors underlying *Coregonus* spp. year-class strength variation includes density-independent physical environmental factors such as annual weather patterns that affect larval fishes directly or their food (Axenrot and Degerman 2015), density-dependent biotic factors (e.g., predation by or competition with Rainbow Smelt; Myers et al. 2015) or spawner sex ratios (Bunnell et al. 2006), or a combination of these factors. Synchrony among disjunct populations and between species in the same region supports the idea that environmental factors such as winter ice conditions, spring ice break-up date, and wind play a major role in determining year-class strength of *Coregonus* spp.

Our results indicate that Lake Superior Kiyi are long-lived and exhibit high interannual variability in year-class strength that may be synchronous with recruitment patterns exhibited by other *Coregonus* spp. The critical period for survival (*sensu* Hjort 1914; Houde 2008) appears to be prior to age-1 as distinct year-classes observed at age-1 appeared to survive to older ages. While currently not commercially or recreationally valuable like some *Coregonus* spp., Kiyi are a key trophic link between zooplankton and Lake Trout *Salvelinus namaycush*, the top native predator in the Great Lakes (Gamble et al. 2011), which is a commercially and recreationally important species. Successful restoration of deepwater ciscoes in the other Great Lakes may depend on understanding their life histories (Zimmerman and Krueger 2009). Additionally, Lake Superior is a refuge for many cold stenothermic species like Kiyi, which is currently listed as vulnerable on Canada's Endangered Species List (Turgeon and Bernatchez 2003). Increased study of and long-term monitoring of Kiyi and other cisco species, including age, growth, diet, and recruitment characteristics, may provide insight into how climate change may affect the deepwater fish fauna of Lake Superior and elsewhere.

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American Fisheries Society guidelines for the care and use of fishes
(<http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf>).

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Figure Captions

Figure 1. Sampling locations in Lake Superior and the five regions used for subsampling Kiyi for age estimation in 2014. Squares denote offshore sites and circles denote nearshore sites. Solid symbols denote locations where Kiyi were collected.

Figure 2. Thin-sectioned otolith from a 206-mm male Kiyi captured at an offshore site in the northern Ontario region on 20-Jul-2014 that was estimated to be 11 years old. The length of the white bar is 1 mm.

Figure 3. Mean (points) and range (vertical intervals) of differences in scale-derived age estimates for Lake Superior Kiyi between two readers by age estimates for the first (more experienced) reader. All fish were collected from the eastern Michigan region (Figure 1). Closed points indicate that the age estimates are either not statistically significant different between readers or the sample size was too small (<3) to test for a difference. The top histogram is the sample size for scale-derived age estimates for the first reader and the right histogram is the distribution of difference in scale-derived age estimates between readers.

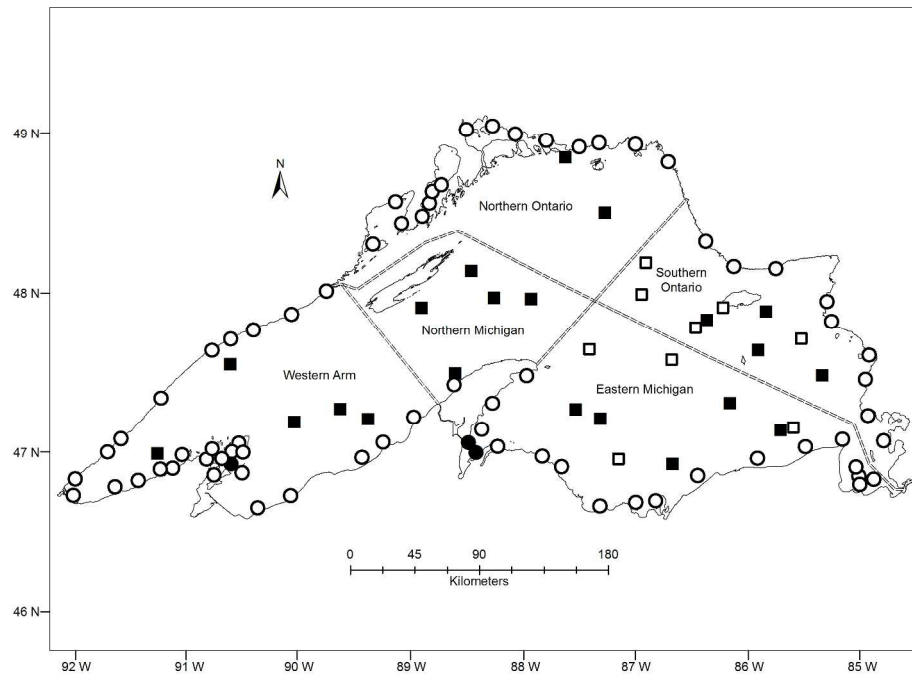
Figure 4. Mean (points) and range (vertical intervals) of differences in otolith-derived age estimates for Lake Superior Kiyi between two readers by age estimates for the first (more experienced) reader. Closed points indicate that the age estimates are either not statistically significant different between readers or the sample size was too small (<3) to test for a difference. The top histogram is the sample size for otolith-derived age estimates for the first reader and the right histogram is the distribution of difference in scale-derived age estimates between readers.

Figure 5. Mean (points) and range (vertical intervals) of differences in scale- and otolith-derived age estimates for Lake Superior Kiyi by otolith-derived age estimates. Closed points indicate that the age estimates are either not statistically significant different between structures or the sample size was too small (<3) to test for a difference. The top histogram is the sample size for otolith-derived age estimates and the right histogram is the distribution of differences between scale- and otolith-derived age estimates.

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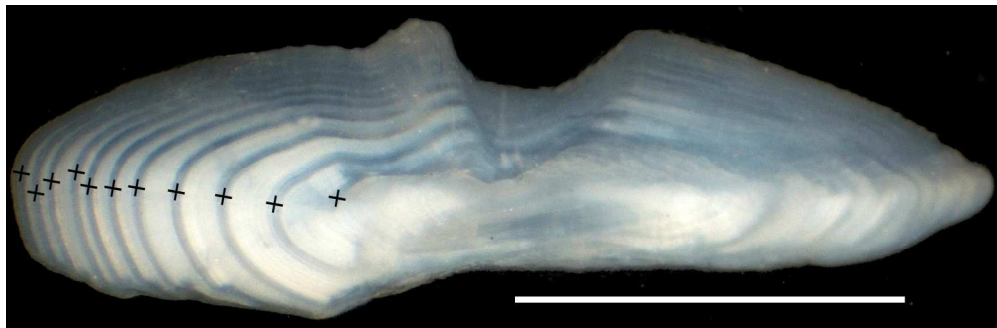
504 Figure 6. Frequency of otolith-derived age estimates for all Lake Superior Kiyi captured from
505 May-July 2014. Ages were expanded from an age-length key based on consensus otolith-derived
506 age estimates between two readers.

507 Figure 7. Relative within-year frequency of total length for all Lake Superior Kiyi captured in
508 May-July from nearshore locations in 2003-2010 and both nearshore and offshore locations in
509 2011-2014. Plots are labeled with the year sampled and the total sample size. Each plot is scaled
510 such that the mode has a height equal to 1. Numeric labels in 2004, 2006, and 2010 are the age
511 fish in those modes were in 2014. The dashed vertical line in each plot at 110 mm was used to
512 identify the total length mode for age-1 fish.



Sampling locations in Lake Superior and the five regions used for subsampling Kiyi for age estimation in 2014. Squares denote offshore sites and circles denote nearshore sites. Solid symbols denote locations where Kiyi were collected in 2014.

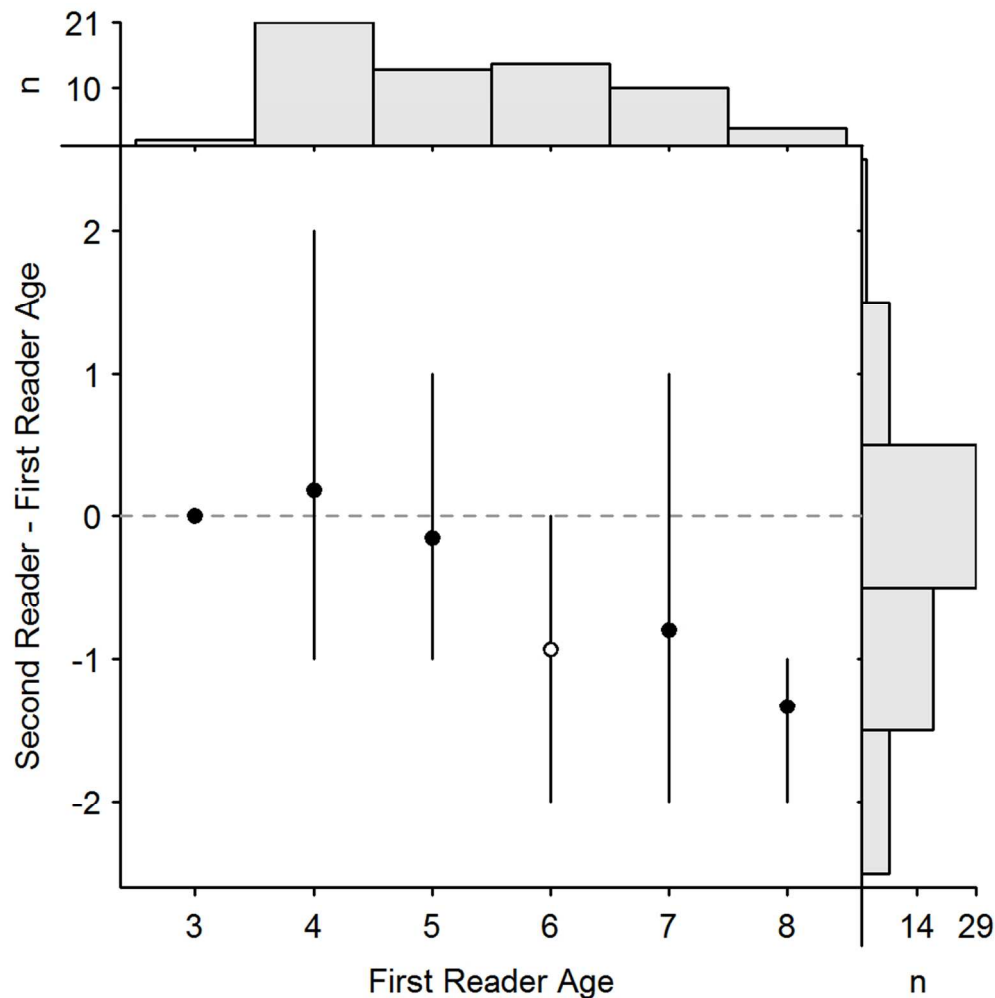
1164x899mm (72 x 72 DPI)



Thin-sectioned otolith from a 206-mm male Kiyi captured at an offshore site in the northern Ontario region on 20-Jul-2014 that was estimated to be 11 years old. The length of the white bar is 1 mm.

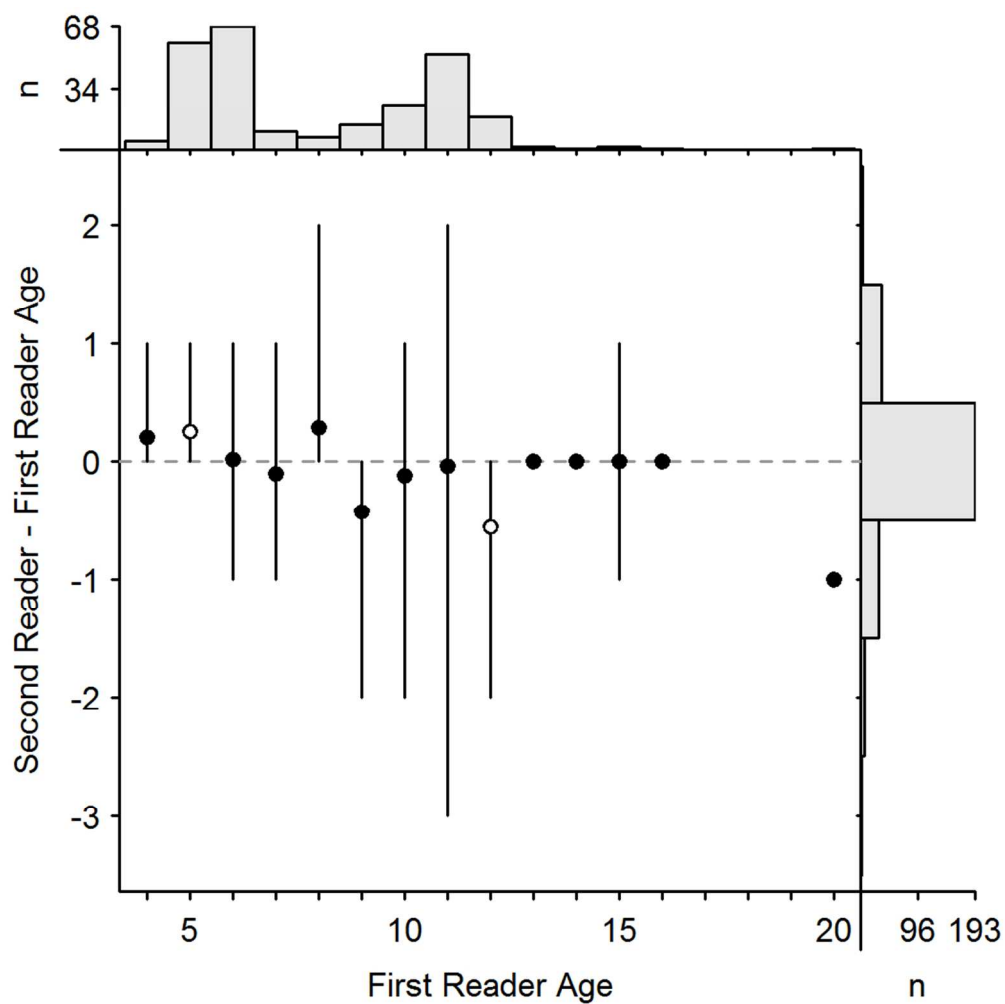
760x246mm (72 x 72 DPI)

Peer Review Only



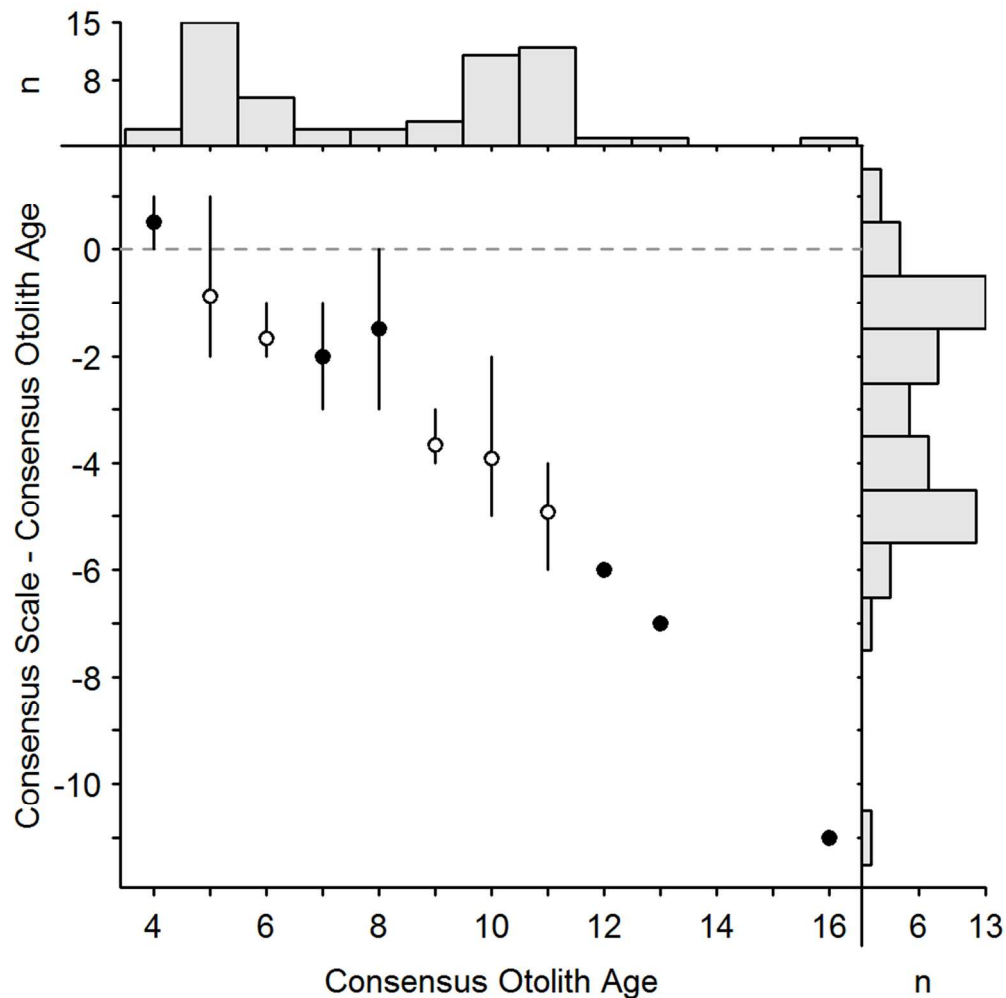
Mean (points) and range (vertical intervals) of differences in scale-derived age estimates for Lake Superior Kiyi between two readers by age estimates for the first (more experienced) reader. All fish were collected from the eastern Michigan region. Closed points indicate that the age estimates are either not statistically significant different between readers or the sample size was too small (<3) to test for a difference. The top histogram is the sample size for scale-derived age estimates for the first reader and the right histogram is the distribution of difference in scale-derived age estimates between readers.

88x88mm (300 x 300 DPI)



Mean (points) and range (vertical intervals) of differences in otolith-derived age estimates for Lake Superior Kiyi between two readers by age estimates for the first (more experienced) reader. Closed points indicate that the age estimates are either not statistically significant different between readers or the sample size was too small (<3) to test for a difference. The top histogram is the sample size for otolith-derived age estimates for the first reader and the right histogram is the distribution of difference in scale-derived age estimates between readers.

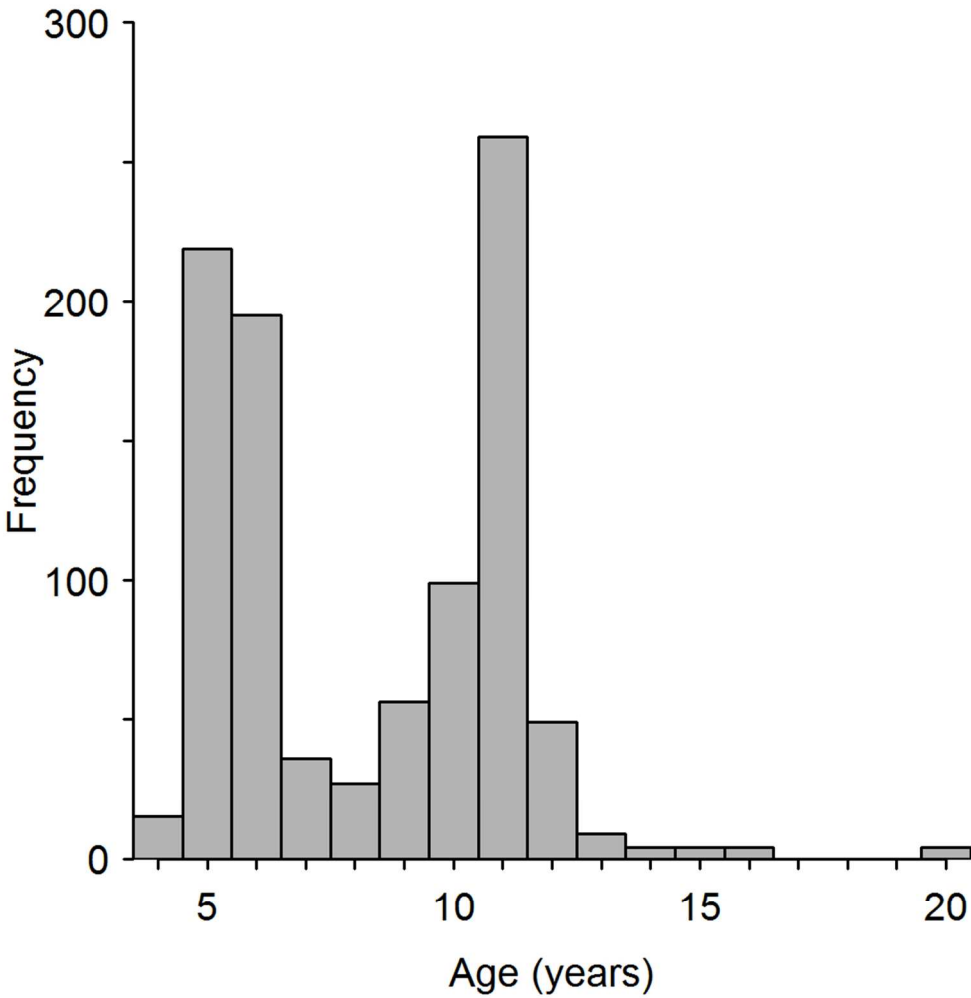
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Mean (points) and range (vertical intervals) of differences in scale- and otolith-derived age estimates for Lake Superior Kiyi by otolith-derived age estimates. Closed points indicate that the age estimates are either not statistically significant different between structures or the sample size was too small (<3) to test for a difference. The top histogram is the sample size for otolith-derived age estimates and the right histogram is the distribution of differences between scale- and otolith-derived age estimates.

88x88mm (300 x 300 DPI)

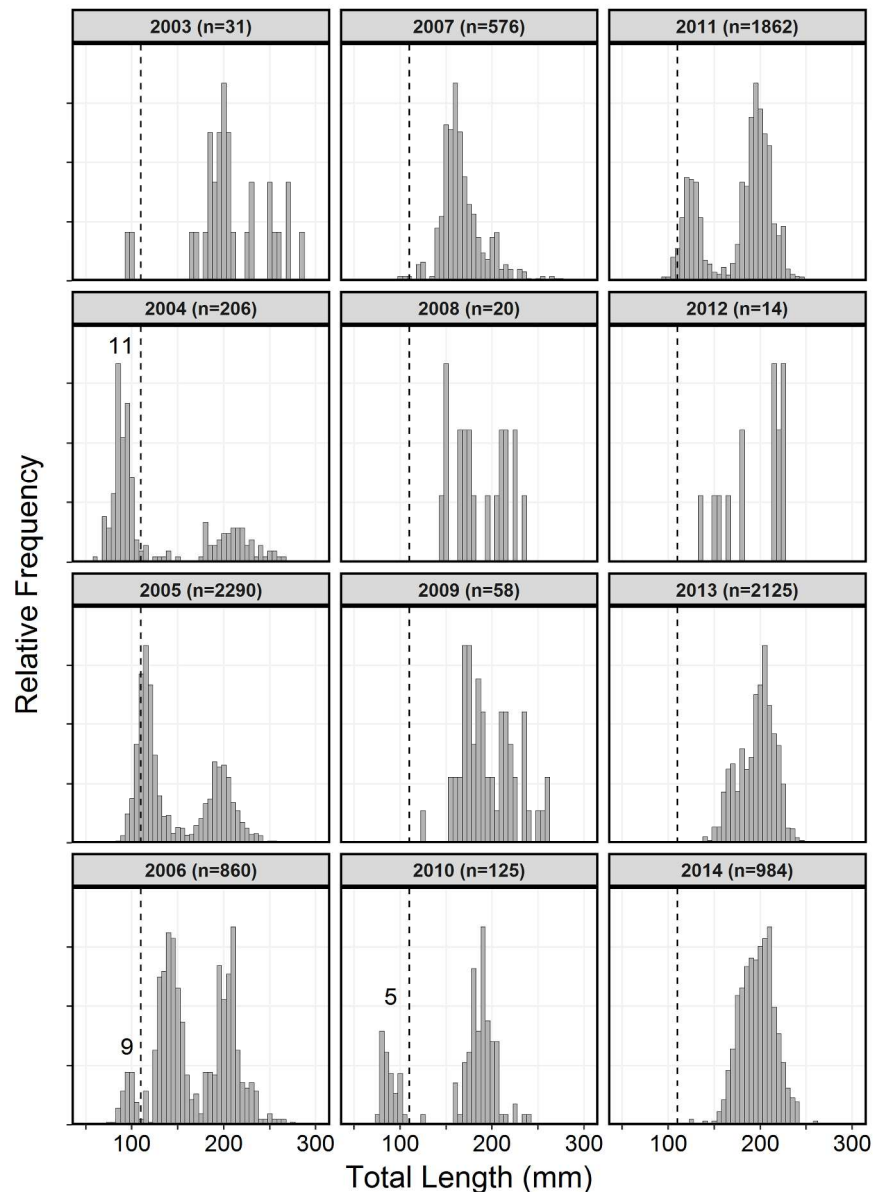




Frequency of otolith-derived age estimates for all Lake Superior Kiyi captured from May-July 2014. Ages were expanded from an age-length key based on consensus otolith-derived age estimates between two readers.

88x88mm (300 x 300 DPI)





Relative within-year frequency of total length for all Lake Superior Kiyi captured in May-July from nearshore locations in 2003-2010 and both nearshore and offshore locations in 2011-2014. Plots are labeled with the year sampled and the total sample size. Each plot is scaled such that the mode has a height equal to 1. Numeric labels in 2004, 2006, and 2010 are the age fish in those modes were in 2014. The dashed vertical line in each plot at 110 mm was used to identify the total length mode for age-1 fish.

184x254mm (300 x 300 DPI)

Reviewer: 2

Comments to the Author

The management brief entitled "Age, year-class strength variability, and partial age validation of *Coregonus kiyi* from Lake Superior" has been revised appropriately and all major concerns have been addressed. I feel that the manuscript has been improved substantially.

By adding one additional scale reader, I feel that the authors have adequately addressed the concern that only one reader estimated scale ages in the study. I believe this has improved the quality of the manuscript. Admittedly, I am still puzzled by the authors' reluctance to use the full data set, a suggestion I made in my initial review of the brief. I was not clear in my second-round review by using the phrase "similar number of scales and otoliths." My intention was to point out that the same number of scales and otoliths should be read because, as the author has indicated, these are paired structures. In fact, in their rebuttal, the authors state that "to compare scales and otoliths, there must be the same number of scales and otoliths read as they are paired observations." In my first round review of this brief, I indicated that if the full data set was available (i.e., all scales and otoliths from all 288 fish) using all of these observations to compare otolith and scale ages would build a much stronger case than using a subset of scale ages. Again, I feel the manuscript has been improved but want to be clear in my purpose for bringing this up.

By addressing the length frequency analysis in the discussion the authors have sufficiently addressed my concern with potentially lumping age classes.

RESPONSE: We thank the reviewer for clarifying his/her previous comment.

Associate Editor Comments to the Author:

Comments to the Author:

I commend the authors for improving their manuscript. The reviewer and I have found that our concerns have been addressed. I thank you for bolstering your methods to address my last round of critiques. I do want to provide a few, final and minor suggestions for edits that should be easy to do:

lines 20 and 199: Suggest re-word slightly to avoid the noun train, "Kiyi length frequency data"

RESPONSE: Done.

Fig. 1: Consider omitting, 'were collected in 2014'--I believe this is already implicit.

RESPONSE: Partially done. We omitted "in 2014" but left "were collected".

Fig. 2: I should've mentioned this last time. I appreciate the inclusion of this figure; I think it is incredibly informative and useful.

RESPONSE: Thank you.

Fig. 3: Caption: Please cite '(Figure 1)' after indication of the 'eastern Michigan region'

RESPONSE: Done.

Line 56: Citations of Maceina and Quist are adequate. Please consider also including citation(s) of ageing work done on lake whitefish by Andrew Muir et al. People searching his papers may be more likely to find yours in this connection.

RESPONSE: We did not add the Muir et al. papers here. The Maceina and Quist citations are meant to illustrate that this is a general phenomenon. Adding Muir et al. would provide a specific example that would either lead to more specific examples or a question from the readers about why there are not other specific examples. We did cite one Muir et al. paper in the discussion and we have now added reference to a second Muir et al. paper in the discussion. Thus, we think that people searching for his papers will still be more likely to find our paper, even without the suggested mention in the introduction.

Note that this resulted in slightly new wording in the paragraph in the discussion that begins with “Kiyi ages estimated from otoliths” (near line 230).

We also thank the AE for bring to our attention that we had missed the second Muir et al. paper. We were certainly aware of it and it was an oversight on our part not to include it.

Line 117: In literally 1-3 words each, please define what constitutes 'considerable' vs. 'little' previous experience in estimating ages.

RESPONSE: Done.

lines 128-129: How many fish were removed from the analysis?

RESPONSE: We ended up reaching a consensus on all fish; thus, no fish were removed from the analysis. This is now reflected in the manuscript (see last sentence of the paragraph in the methods that begins with “Two readers, who were blind to” (near line 125).

Lines 227-232: Consider including citation(s) from lake whitefish work by Andrew Muir et al.

RESPONSE: Done and response to previous comment about line 56.